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THE EMBRYO OF THE ANGIOSPERMS.

HAROLD L. LYON.

THE angiosperms are the dominant plants of present floras, and were the first to be thoroughly studied by botanists. The seed habit, providing a definite period for embryonic development, and the large embryos, often obtaining as a result, made the embryology of the angiosperms especially easy and attractive. Simple lenses and primitive technique served for the study of these embryos, and a knowledge of them was well advanced before better instruments and better methods were employed to elucidate the embryogeny of lower forms.

The angiospermous embryo was early hit upon as furnishing fundamental data for systematic classification. This quickly brought such embryos into prominence in botanical literature, and controversies immediately arose as to the morphological values and homologies of the embryonic members. While a creed, serviceable and satisfactory to the systematists, was soon evolved, the chief questions in morphology have continued to the present day quite unanswered. The aspect of the problem has changed from time to time with increasing knowledge and if we would now attempt a solution we must strive to answer the three following questions.

Are the angiosperms monophyletic ?

Are cotyledons true leaves ?

To what structure, if any, in the monocotylous embryo are the cotyledons of a dicotylous embryo equivalent ?

An answer to the last question is, of course, the one most generally desired ; but to discuss this question one must take some position as to the phylogeny of the classes of angiosperms and to the morphological value of cotyledons.

ARE THE ANGIOSPERMS MONOPHYLETIC ?

It had been so generally conceded that the angiosperms have a common ancestry that in a former paper the writer (: 02) dismissed this question with the following brief statement, "That the Monocotyledons and Dicotyledons have a common ancestry there is no reason to doubt. One would hardly suppose that the similar complicated cytological phenomena of embryo-sac development and endosperm formation were simply parallelisms in two groups of different phylogenetic origin." Later, however, Balfour (:01) in discussing the phylogeny of the angiosperms, said, "Were I to maintain an opinion it would be that the two classes have arisen on separate lines of descent. The embryo characters as well as those of the epicotyl can, I think, be shown to be fundamentally different and to afford no basis for an assumed phyletic connection."

Since Balfour, Coulter and Chamberlain (:03) have written on the same subject as follows: "The first phase of the problem has to do with the common or independent origin of the Monocotyledons and Dicotyledons. It has been assumed generally that the two groups are monophyletic. The chief argument, and in fact the only morphological one for the monophyletic theory, lies in the great uniformity of the peculiar development of both male and female gametophytes. It is argued that the independent origin of such exact details of development and structure is inconceivable, and this argument has been reënforced recently by the discovery in both groups of the peculiar phenomenon called 'double fertilization.' The argument is certainly a very strong one, and yet there are rebutting propositions. Even such similarity in structure may be the natural outcome of the changes that resulted in the evolution of seeds, and these are now generally believed to have appeared in independent lines. Again, the fundamental differences in the development of the embryos of the two groups are hard to reconcile upon the theory of monophyletic origin. Add to this the fundamental differences in the structure of the stem and in the character of its vascular bundles, and the derivation of one group from the other seems more inconceivable than the derivation of the Dicotyledons from the Gymnosperms. Still another argument against the monophyletic theory is furnished by the historical testimony. The Proangiosperms of the Lower Cretaceous, so far as known, appeared associated with undoubted Monocotyledons, and merged gradually into recognizable Dicotyledons. The emerging of Dicotyledons from this vague group either indicates that Monocotyledons and Dicotyledons originated independently, or that the Proangiosperms were transition forms between Monocotyledons and Dicotyledons. This latter alternative is in turn inconceivable, especially since the most primitive Dicotyledons are recognized to be even more primitive than any of the Monocotyledons. . . . . In our judgment the evidence is strongly in favor of the independent origin of the two groups, which have attained practically the same advancement in the essential morphological structures, but are very diverse in their more superficial features. Their great distinctness now indicates either that they were always distinct or that they originated from forms that were really Proangiosperms and neither Monocotyledons nor Dicotyledons."

Few morphologists will agree with the statement that the only morphological argument in favor of the monophyletic theory is to be derived from the similarity in embryo and endosperm development. There is in both classes a remarkable conformity to one common plan in all phases of their organogeny; not only in the embryo-sac, but in the development of floral structures, androecia, gynoecia, ovules, seeds and fruits. While many similarities in plant structures have undoubtedly resulted through parallel development, is it not carrying the idea to an unwarranted extreme when it is attempted to explain all the exact details of development, which obtain alike in both classes of Angiosperms, as simply parallelisms, especially since no tangible evidence is brought forward to justify it?

If the fundamental differences in embryogeny are to be delineated by the exceptionally perfected embryos of Alisma and Bursa, as is so generally stated, they might be considered hard to reconcile. If on the other hand they are to be determined by a comprehensive comparison of the various types of embryos to be found in the two classes, the real difficulty is not, how to reconcile these differences, but how to locate them. An examination of recent embryological work[1] will show that no *funda-*

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[1] Sterckx ('99), Lyon (:01), Cook (:02), Schmid (:02), Sargant (:02, :03, :04), Schaffner (:04), York (:04).

mental differences can be distinguished. Coulter and Chamberlain themselves in a previous chapter of the same work, write, "The distinction between Monocotyledons and Dicotyledons is not always clear in the embryo."

Should fundamental differences in the structure of the stem and its vascular bundles be pointed out, this "*rebutting proposition*" might prove a serious one. It is certain, however, that such an opinion can carry little weight when opposed to the conclusions of careful investigators supported by their researches. And almost without an exception, students[1] who have actually worked on the stem anatomy of the angiosperms with a view to determining their phylogeny, concur in the opinion that here also the evidence is for and not against a monophyletic origin. There is a characteristic type of stem and bundle structure prevalent in each class it is true, but in certain plants of both they so closely approximate a common type that no hard and fast line can be drawn between the classes on this basis. That both types have been evolved within the angiosperms from one fundamental pattern is amply demonstrated by existing plants as the above mentioned students have shown. Coulter and Chamberlain (: 03) would place the Nymphæaceæ among the dicotyledons because of their embryo-characters; but no one has ever been able to show that the stem structure of the Nymphæaceæ is other than essentially that characteristic of monocotyledons. In placing the Nymphæaceæ as they do, they themselves admit that there are no differences in stem structure between the plants of the two classes which are fundamental.

As to the historical testimony which is to be derived from palæobotany, Seward (: 03) has shown that, in the extent of our present knowledge, it is to be considered of questionable value.

While giving due consideration to these adverse opinions; admitting that an independent origin of the monocotyledons and dicotyledons is not inconceivable, and that all their common morphological, structural and cytological peculiarities might be simply parallelisms; still we are justified in accepting the strongly fortified conclusion, borne out by all obtainable evidence, that the angiosperms are monophyletic ; that their most recent common ancestors were Angiosperms.

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[1] Queva ('99), Jeffrey (: 00, : 03), Worsdell (: 02), Sargant (: 03).

ARE COTYLEDONS TRUE LEAVES?

The oldest and at all times the favorite interpretation of cotyledons is that they are arrested or metamorphosed foliage leaves. The antiquity of this view as well as the basis on which it was founded is well set forth in the following quotation from Sachs' *History of Botany*.[1] "We see that Cesalpino uses the same word 'folium' without distinction for calyx, corolla and ordinary leaves ; just as he and Malpighi a hundred years later unhesitatingly regarded the cotyledons as metamorphosed leaves. In fact the envelopes of the flower and the cotyledons approach so nearly to the character of leaves that every unprejudiced eye must instinctively perceive the resemblance."

From time to time various authors, while accepting the foliar theory of cotyledons in its general application, have concluded that the analogous structures in certain plants are not true cotyledons but organs of a different morphological value. The scutellum of the grasses, which is now commonly considered a cotyledon, has been variously interpreted.[2] Richard ('11) distinguished as 'Embryons macropodes' the embryos of the grasses, Nelumbo, Ruppia, Hydrocharis and Zostera. The scutellum of the grass embryo and the cotyledonary lobes of the embryo of Nelumbo he considered homologous to the massive, macropodous portions (l'hypoblaste) of the embryos of Ruppia, Zostera and Hydrocharis. This hypoblast he interpreted as a lateral outgrowth or expansion of the radicle. Schaffner (:04) compares the embryos of the Nymphæaceæ with those of Ruppia, Zostera and Halophila. He reiterates Richards conclusions concerning the homology of the cotyledonary lobes with the macropodous body which he terms a hypocotyledonary expansion.

Nageli ('78), however, early ventured the opinion that "Der Embryo der Gefässkryptogamen und der Phanerogamen ist kein Caulom sondern ein Thallom, wie das Moossporangium, aus dem er phylogenetisch hervorgegangen ist; die Samenlappen sind keine Phyllome, sondern Thallomlappen. An dem Embryo tritt als neue Bildung der Stengel auf."

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[1] English translation 1890, p. 48.

[2] *Vide* Bruns ('92) and Kennedy (:00).

In a lecture delivered at the Minnesota Seaside Station in June, 1901, and since published in the Year Book of the station, the writer suggested that cotyledons are not arrested leaves but are primarily haustorial organs, originating phylogenetically as the nursing-foot in the Bryophyta and persisting throughout the higher plants.

Balfour, in his presidential address to the Botanical section of the British Association, September meeting, 1901, said, "We ought, I think, to look upon the embryo of the angiosperms as a protocorm of embryonic tissue adapted to a seed life. Under the influence of its heterotropic nutrition and seed environment it may develop organs not represented in the adult plant, as we see in, for instance, the embryonal intra-ovular and extra-ovular haustoria it often possesses. There is no reason to assume that there must be homologies between the protocorm and the adult outside an axial part with its polarity. There may be homologous organs. But neither in ontogeny nor in phylogeny is there sufficient evidence to show that the parts of the embryo are a reduction of those of the adult. . . . . I cannot pursue the subject here nor discuss the view of the cotyledons as either ancestral leaf-forms or arrested epicotylar leaves. The analogies with existing Pteridophytes that are cited are not pertinent, for there is no evidence that angiosperms have that ancestry, or indeed that their phylogeny was through forms with free embryos. Nor is the fact of resemblance between cotyledons and epicotylar leaves and the existence of transitions between them convincing. That the cotyledons, primarily suctorial organs, should change their function and become leaf-like under the new conditions after germination is no more peculiar than that the hypocotyl should take the form of an epicotylar internode from which it is intrinsically different as the frequent development upon it of hypocotylar buds throughout its extent shows."

While each of the above authors expresses a distinct interpretation quite at variance with those offered by the others, still all declare alike on our present point of discussion, that cotyledons are not morphologically foliage-leaves.

Ramaley (: 02), who for the past ten years has been working on the comparative anatomy of dicotyledonous seedlings, expresses his opinion on this subject in the following statement: "I think also that the theory of the above named writer [Preston, : 02] to account for the lobing of cotyledons is of no great value. He suggests that the lobing of the foliage leaf is 'thrown back' upon the cotyledon. This assumes firstly that 'throwing back' can actually occur, while as a matter of fact it yet remains to be proven; and secondly, that the cotyledons are homologous with leaves, something which also remains unproven. The suggestion[1] concerning the morphology of the cotyledon made at the recent Chicago meeting of botanists of the central states seems more reasonable than the one which would consider the cotyledons as really a leaf."

Many other writers have expressed dissatisfaction with the foliar theory without taking a decided stand against it. Klebs ('83) in his excellent treatise on germination pronounces the subject an enigma, while Lubbock ('92), who has undoubtedly made more extensive observations upon seedlings than any other one man, writes: "No one who has ever looked at young plants can have failed to be struck by the contrast they afford to the older specimens belonging to the same species. This arises partly from differences in the leaves, partly from the contrast which the cotyledons, or seed-leaves, afford, not only to the final leaves, but even to those by which they are immediately followed. This contrast between the cotyledons and true leaves is so great that one might almost be pardoned for asking whether they can be brought in correlation. So far, indeed, are the cotyledons from agreeing with the forms of the leaves, that the difficulty is to find any which have been clearly influenced by them. One species of Ipomœa (I. Pes-capræ) has both cotyledons and leaves, as the name denotes, somewhat like the foot of a goat; but the leaves vary considerably, and it is probable that the resemblance may be accidental. A clear case is, however, afforded by the Onagrarieæ, where in Œnothera and some allied genera the form of the mature cotyledons is evidently related to the leaves. Even here, however, the resemblance is confined to a basal portion of the cotyledon which makes its appearance subsequent to germination, and no trace of it is shown in the cotyledons themselves when they first appear."

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[1] Lyon (: 02).

We can readily see from Lubbock's work that a morphological leaf-value has been ascribed to cotyledons solely on their resemblance to foliage leaves, a resemblance which is acquired after germination when the cotyledons are functioning as photosynthetic areas. Then they are only in general leaf-like, for if any cotyledons be compared with the foliage leaves of the same plant they are found to differ from these, usually to a marked degree in form, texture and venation. The resemblance is never more than such as might be wholly induced by the assumption of the vegetative function, for the cotyledons become functionally similar structures in the same environment as the leaves. Natural forces seem to call forth a remarkably constant type of foliar organ in all those plants where any extent of tissue is specialized for this purpose no matter what the morphological value of the tissue may be. The gametophytes of some mosses develop leaves which are quite similar to the simpler leaves produced by the sporophytes of many pteridophytes and phanerogams. Phyllodes and Phylloclades are well known cases where the assumption of the function has, in many instances, been followed by the assumption of the form of leaves.

Ramaley has undertaken a study of the comparative anatomy of cotyledons and leaves. In his paper (:03) on the cotyledons and leaves of the Papilionaceæ, he writes: "In the plants examined, all of which have cotyledons which function for a time as leaves, the anatomical structure is strikingly different in cotyledons and leaves. . . . . The stalk of the cotyledon when present has a structure different from that of the leaf-stalk." Again (:04) he writes: "In the Ranunculaceæ and Cruciferæ studied there is not as great a difference in structure between cotyledons and leaves as was seen in the Papilionaceæ. . . . . The stalks of the cotyledon and leaf are quite different in anatomical structure. . . . . In these families as in the Papilionaceæ there seems to be no relation in external form between the cotyledon and leaf."

The ontogenetic origin of the cotyledons would seem to deny the foliar theory since they do not arise as exogenous lateral outgrowths upon the growing point of the stem as do all later foliar structures. Their appearance always precedes the differentiation of the stem-apex.

Thus it appears that the foliar theory is supported only by the fact that in some plants the cotyledons are borne on a stem and are green, and may acquire a form resembling a leaf. It seems certain that any "unprejudiced" observer must at once admit that these are but superficial analogies; quite insufficient evidence to warrant the conclusions so universally based upon them.

To what Structure, if any, in the Monocotylous Embryo are the Cotyledons of a Dicotylous Embryo Equivalent?

Early embryologists considered the cotyledons of all angiosperms (with the exceptions already noted) to be structures of the same category, morphologically as well as physiologically, and their conclusions have been accepted by botanists in general.

Balfour (:01), however, states that, "This terminal cotyledon in the Monocotyledons is not a leaf nor the homologue of the lateral cotyledons in the Dicotyledons."

In this opinion he is again supported by Coulter and Chamberlain (:03): "The current opinion regards it [the cotyledon] as a modified foliage leaf, and this is borne out in the majority of Dicotyledons by the assumption of the foliage function. The terminal cotyledon of Monocotyledons, however, seems to belong to a different category, and to hold no relation to a foliage leaf or to a foliar member of any description." To discover evidence which will in general prove the homology of the cotyledons, one has but to consult the recent works of Sterckx ('99), Lyon (:01), Cook (:02), Schmid (:02), Sargant (:02, :03, :04), Schaffner (:04) and York (:04). Just as the observations of the above mentioned investigators dispel all idea of such fundamental differences in the embryos as would indicate two types of different phylogenetic origin, so also do they show clearly that the cotyledons of the angiosperms are morphologically of one category. In 1809 Poiteau published the theory that the epiblast of certain grasses represents a vestigial cotyledon thus indicating a dicotyledonous origin for these plants. This hypothesis has won many adherents and but recently Van Tieghem ('98) has, on the strength of it, placed the Grasses with the Nymphæaceæ under a third class of angiosperms which he calls Liorhiza dicotyledons. Van Tieghem's classification has been adequately dealt with by Balfour (:01, :02) and needs no further attention from us at this time. Poiteau's idea of the reduction of one cotyledon was employed by Henslow ('93) to explain the origin of the monocotylous condition throughout the Monocotyledons.

Agardh ('29–'32) also accepted Poiteau's interpretation of the grass-embryo but considered the Gramineæ the only true monocotyledons. The Naiadeæ, Palmæ, Aroideæ, Lilieæ and Scitamineæ, and probably other families of monocotyledons, he classed as syncotyledones, considering the terminal structure of their embryos to represent two cotyledons which had become fused into a single member.

In a previous paper, the writer (:02) also concluded that the cotyledon of a monocotyledon was equivalent to both of the cotyledons of a dicotyledon, but that the monocotylous condition was the more primitive and that from this the dicotylous condition had arisen through a bifurcation of the originally single cotyledon. The morphological value ascribed to the cotyledon led primarily to this conclusion which was further strengthened by embryological studies in the Nymphæaceæ.

In a series of admirable papers, Miss Sargant (:02, :03, :04) has brought together much evidence, of which her own research work has furnished a very important part, showing that the cotyledon of a monocotylous embryo is equivalent to both of the cotyledons of the dicotylous embryo. Add to this the evidence from the Nymphæaceæ embodied in the recent works of Lyon (:01), Cook (:02), Schaffner (:04), and York (:04) and the conclusion would seem a necessity. In considering the phylogeny of the angiosperms, however, Miss Sargant has accepted the view suggested by Agardh, that the monocotylous condition has been derived from the dicotylous condition through the fusion of two cotyledons into a single member. Thus while the relative value of the cotyledons in the two classes needs no further discussion at this time, we have yet to choose between the hypothesis elaborated by Miss Sargant and the one suggested by the writer.

It is obvious that the anatomical and morphological evidence collected by Miss Sargant can as readily be interpreted in support of the writer's hypothesis as the one brought forward by herself. It can quite as well be interpreted as showing a transition from the monocotylous to the dicotylous condition by a bifurcation of the cotyledon, as demonstrating a reduction from the dicotylous to the monocotylous condition through a fusion of two cotyledons. It can be read forward as well as backward. Progression in evolution is quite as plausible as retrogression, yet Miss Sargant hopes to convince her readers with the following unique argument: "To conceive of steps by which two separate cotyledons should gradually unite is easier than to imagine a single cotyledon splitting into two similar members as suggested by Mr. H. L. Lyon."

While Miss Sargant is able to cite some thirty dicotyledonous seedlings as having their cotyledons partially or completely united into a single member, one might easily mention a hundred dicotyledonous seedlings having their cotyledons deeply emarginate, bifid or even bipartite. Then cotyledons deeply three-lobed, four-lobed, and five-lobed are not unknown. In various species of Acer, seedlings with three and four distinct cotyledons are of frequent occurrence. *Pittosporum crassifolium* produces three or four cotyledons quite as often as two, while *Nuytsia floribunda* habitually produces embryos with three or four cotyledons. Would the writer propound an inconceivable hypothesis were he to suggest that in these dicotyledons the variously lobed and polycotyledonous conditions had arisen through a splitting of cotyledons; or must he adopt that "easier" line of reasoning and maintain that the polycotyledonous condition is the more primitive, and that the dicotyledonous condition has been arrived at through a reduction by the gradual union of the many members into two? All morphologists will affirm that this lobing of the cotyledons has resulted through adaptation to the various conditions imposed by the seeds. Might not these same causes, whose effect on two cotyledons is so often apparent, have primarily induced the division of a single cotyledon into two? In considering divided cotyledons, Lubbock ('92), concludes that the bifurcation of the cotyledons in such plants as Eschscholtzia and Schizopetalon are adaptations whereby the cotyledons are better able to free themselves from the seed. If for this purpose four cotyledons are superior to two, in what far greater proportion are two cotyledons superior to one?

Although its evidence can never be taken as absolute, still we are justified in placing some value on recapitulatory development. If the monocotylous condition arose through the union of two cotyledons we might reasonably expect to find, in our transition-types, that two distinct cotyledon-primordia would first appear, and conjoint development occur later. Such a sequence we actually find in the development of gamophyllous perianths. But in all the anomalous forms cited by Miss Sargant, of which the embryogeny has been studied, a single primordium first appears which, if the cotyledon is to become lobed at all, later bifurcates.

In her first paper on this subject, Miss Sargant (:02) attributed the reduction of the cotyledons to their specialization as a sucking organ. Of the monocotyledons, she writes, "I have regarded them for some time as specialized forms of an ancestor with two seed-leaves. The complete union of the cotyledons may very possibly be due to their common specilization as a sucking organ. It is true that all cotyledons begin life by absorbing nourishment from a food-body within the seed, but in dicotyledonous seedlings they commonly lay aside that function at an early period, even though they may never become assimilating organs. Among Monocotyledons on the contrary, the apex of the cotyledon often remains within the endosperm throughout the existence of both, a period which covers years in palms and some other plants. Such a habit as this would naturally lead in course of time to the fusion of the cotyledons within the seed." This hypothesis would seem to maintain that the specialization in seeds has been from the exalbuminous towards the albuminous condition. This supposition however meets with immediate denial from our knowledge of the phylogeny of seeds.

In her later papers, Miss Sargant (: 03, : 04) fails to reiterate the above hypothesis of the reduction factor but says : "These considerations have led me to look upon the Monocotyledon as an organism adapted primarily to a geophilous habit," and "Suppose a race of primitive Angiosperms to be specialized as geophytes. Their originally distinct cotyledons become more and more closely united in order to economize material. In the end a single cotyledonary member is formed by their complete fusion. A monocotyledonous race might easily be derived in this way from one with two cotyledons." While it is possibly true that the development of cotyledonary tubes has resulted in some dicotyledons through adaptation to a geophilous habit; just how this habit might have caused a fusion and subsequent reduction of the blades of the cotyledons, Miss Sargant does not make clear in any of her papers; and how the habit should finally force the cotyledon into the subterranean position characteristic of monocotyledons receives no explanation at all. Furthermore, her hypothesis would seem to require that the primitive angiosperms were not geophytes. It is now commonly held that the angiosperms are the progeny of pteridophytic ancestors, and it might be well to consider that the geophilous habit is quite prevalent among the Pteridophyta.

Finally, the entire structure of Miss Sargant's theory is built upon the assumption that cotyledons are morphologically foliage-leaves. But we have already found that this assumption is disproved by our knowledge of the form, structure, and development of cotyledons. To make her theory seem tenable, Miss Sargant must first make plausible this assumed premise on which the validity of her hypothesis so largely depends.

RECAPITULATION.

The great value ascribed to the embryo in the systematic classification of the Angiosperms early brought such embryos into prominence in botanical literature. Thus we find that angiospermic embryology embodied an extensive knowledge before any careful work had been done on the cryptogams. As a result an interpretation of the angiospermic embryo was evolved wholly from evidence obtained from angiosperms and without reference to any evidence which cryptogamic embryos might furnish. This interpretation in the hands of the systematists soon became a fixed creed which has come down to the present day as built upon facts too well established to be questioned. Some morphologists have, it is true, attacked this creed, but have failed to lessen in the slightest degree its general acceptance.

Because the cotyledons of certain plants assumed the function and approximated the form of leaves, a morphological leaf-value was, from the first, ascribed to them. This hypothesis, framed on simple analogy, is the self-evident fact which constitutes the basis for all later acceptable embryological considerations. If cotyledons are morphologically foliage leaves, that the most primitive angiosperms must be those of which the cotyledons most nearly approach foliage leaves, is a conclusion which naturally followed. And hence the creed recognized the dicotyledons as the most primitive and considered the monocotyledons a race derived from them. Some theorists would derive the monocotylous condition from the dicotylous, by the abortion of one cotyledon, and others, through the fusion of the two cotyledons into a single member.

Following, and followed by others, the writer has concluded that cotyledons are not metamorphosed foliage leaves. The writer has further suggested that they are primarily haustorial organs originating phylogenetically as the nursing-foot of the Bryophytes and persisting throughout the higher plants; that the monocotylous condition is the more primitive and that the dicotylous condition has arisen through a bifurcation of an originally single cotyledon.

There are, it is true, certain dicotyledons which show a tendency to reduce one cotyledon and others in which a partial or complete fusion of the cotyledon petioles undoubtedly takes place, yet there is no evidence to justify the sweeping application of either process in explaining the origin of the monocotylous condition.

The embryos of the so-called anomalous dicotyledons can as readily be interpreted as demonstrating the bifurcation of one cotyledon as proving the fusion of two, and if we take into account the course of events in their ontogeny they support the former hypothesis in preference to the latter.

While, as mentioned above, some few dicotyledons show a tendency to reduce the cotyledons there is an opposite tendency far more prevalent among dicotyledons to produce lobed, bifid and bipartite cotyledons; undeniably a process of splitting.

Finally if the foliar-theory of cotyledons can be established the writer's entire hypothesis must fall. If the adverse hypotheses are to be proven, the foliar-theory must first be established.

THE PHYLOGENY OF THE COTYLEDON.

In a paper now in preparation, the writer will endeavor to demonstrate the validity of his hypothesis concerning the phylogeny of the cotyledon. A previous paper (:02) on this subject only served to indicate in an indefinite way the scope of the theory. Since that time continued investigations in the field, laboratory and library have yielded evidence which bears out to a remarkable degree the fundamental idea, at the same time furnishing the necessary details for a more exact formulation of the hypothesis. The following outline illustrates the application of this hypothesis to plant embryology.

Cryptogamic embryos. — The first regional differentiation of the body-tissue of the sporophyte was into the spore-containing capsule and the bulbous nursing-foot; the function of the former being the bearing and protection of the spores, that of the latter the absorption of nourishment and the furnishing of mechanical support. Since these two regions form the bases for all later elaboration of the sporophyte we may conveniently assign to them the distinctive names of *sporophore* and *haustrum.* As the haustrum and sporophore are not always distinguishable from the first in the embryo we will find the term *protocorm*[1] quite serviceable as designating the whole embryo before this primary differentiation is complete, and the term *metacorm* for the plant body after the differentiation of its permanent members. All of the protocorm or only a portion of its tissue may be employed in the formation of the metacormal primordia.

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[1] This admirable term was first used by Treub ('88) to designate the "embryonic tubercules" of various lycopods. The writer simply extends the use of the term without seriously altering its original meaning.

In the Bryophyta the haustrum remains embedded in the tissue of the gametophyte throughout its own existence,, but in the Pteridophyta it acquires the habit of anchoring the sporophyte in the soil after the tissue of the gametophyte is exhausted. This seems to have at first resulted in the production of a large, bulbous haustrum (Phylloglossum, *Lycopodium cernuum*) but later some haustral tissue became modified into a distinctive earth-boring organ, the root, a structure much better adapted for penetrating and drawing water from the soil. In *Lycopodium cernuum* the bulbous haustrum may give rise to roots, which in turn may be converted back into bulbous haustra. While some lycopods produce large, bulbous, geophilous haustra, among the pteridophytes, as a rule, a bulbous haustrum is employed only in connection with the gametophyte, the haustral tissue which penetrates the soil being differentiated into a root. Thus the primary bulbous haustrum of the bryophytes becomes differentiated in the pteridophytes into two distinct haustral organs; the nursing-foot or cotyledon — the haustrum of the protocorm, and the root — the haustrum of the metacorm.

The capsular sporophore of the Bryophyta gives place in the Pteridophyta to an axis bearing sporophylls. Because of their position, the photosynthetic work falls upon the sporophylls, and this very soon leads to a division of labor with a consequent sterilization of some sporophylls as foliage leaves or euphylls. While phylogenetically the sporophore precedes the haustrum, the requirements of the former during its development upon the latter, seems to have stimulated an ontogenetic acceleration of the haustrum and a corresponding retardation of the sporophore, so that in ontogeny a functional haustrum precedes the sporophore. Thus in the embryogeny of Anthoceros and Sphagnum we find that of the massive protocorms first developed the greater portion is haustral tissue on which the sporophore stands as a papilla. Among the pteridophytes the ontogenetic acceleration of the haustrum is always apparent so that their protocorms are essentially haustral structures from which the sporophore sooner or later develops as an outgrowth. In Phylloglossum the ontogenetic acceleration of the haustrum is most pronounced, a large bulbous protocorm resulting, from which the sporophore is differentiated at a quite late period (Fig. 2). As the protocorm of this plant becomes geophilous, it develops leaf-like lobes of tissue which carry on photosynthetic work. Bower ('94) terms these protocormal leaves, *protophylls*, to distinguish them from the leaves of the metacorm, the euphylls. With the specialization of the root as the earth-boring haustrum and the euphylls as the photosynthetic areas, the geophilous protocorm with its protophylls disappears from the ontogeny of the higher pteridophytes as we have already found. Perhaps, however, the first leaf of some of these should be interpreted as a protophyll rather than a euphyll.

In the embryogeny of Lycopodium and Selaginella an outgrowth from the protocorm serves to carry the embryo down into the tissue of the gametophyte. This protocormal organ, the suspensor, is limited to the lycopods among the pteridophytes but is of general occurrence in the embryogeny of the angiosperms.

The positional relation which the metacorm bears to the protocorm is remarkably different in different cryptogamic embryos. In the Bryophyta the axis of the metacorm is coincident with the axis of the protocorm, the haustrum of the latter developing into the haustrum of the mature plant. With the advent of the root as the haustral organ of the metacorm, the position in which it is differentiated in relation to the sporophore determines the primary axis of the metacorm. In some embryos the root is differentiated out of the body of the protocormal haustrum, while in others it appears as an outgrowth from this structure. In *Botrychium obliquum* and Equisetum, the root appears diametrically opposite the sporophore and hence the metacormal axis transfixes the protocorm, the tissue of the latter becoming a permanent part of the metacorm. In Selaginella, the metacormal axis is differentiated through the tissue of the protocorm, the suspensor being on one side of the axis, and the cotyledon on the other (Fig. 3). In the leptosporangiate ferns, the sporophore and root appear as adjacent outgrowths from the protocorm thus leaving the haustrum of the latter as a lateral cotyledon on one side of the metacormal axis (Fig. 4).

Angiospermic embryos.— In the embryogeny of an angiosperm, a more or less massive protocorm is developed which may, or may not employ a suspensor. The form of the protocorm varies greatly, depending upon the shape and size of the seed, the extent and vigor of the endosperm, the duration of intraseminal development and the many other peculiar conditions presented by the seed habit. The sporophore arises as an outgrowth from the protocorm and its intraseminal development is, as a rule, quite restricted. The metacormal axis is always differentiated through protocormal tissue. (Figs. 5, 6, and 7.)

In the monocotyledons, the sporophore primordium usually appears as a distinctly lateral outgrowth from the protocorm: but with the establishment of the metacormal axis between the sporophore and root the remaining protocormal tissue stands in a lateral position to this axis and, as a lateral cotyledon on one side of this axis, it functions during germination. As the sporophore primordium of a monocotyledon differentiates into the plumule the adjacent protocormal tissue grows forward around it, often completely enclosing it.

In the dicotyledons, the protocorm early bifurcates and the sporophore primordium arises as an outgrowth between these two cotyledons which closely invest it during intraseminal growth (Fig. 7). In many dicotyledons, a new structure, the hypocotyl, appears in the morphogenesis of the metacorm. The hypocotyl is differentiated between the root and sporophore from tissue which is phylogenetically haustral. During germination it serves to elevate the cotyledons and plumule. The cotyledons upon becoming exposed to the light usually become green and often function for a considerable time as photosynthetic areas. The assumption of the function of foliage leaves leads to the assumption of the form of such leaves, and the cotyledons of some plants approximate to a remarkable degree the form of the later euphylls.

Gymnospermic embryos.— That the gymnosperms in the earlier stages of their embryogeny show a great diversity has been known for a long time. That this diversity is but the more or less restricted following of one general plan has been pointed out by Coulter and Chamberlain (: 03^2). Up to the present time the knowledge of the later stages of their embryogeny has been quite insufficient for determining the morphological values of the embryonic structures. Recent investigation, however, has served to elucidate some of the obscure points, and the interpretation that would now be offered is as follows.

In Ginkgo a large spherical protocorm is developed in the venter of the archegonium. The blastema (metacormal bud) arises as an outgrowth from the deepest seated portion of the protocorm and invades the tissue of the gametophyte by its own growth. The stem and root primordia are both differentiated entirely beyond the bulbous protocorm, the axis of the three members being along one straight line (Fig. 8). Upon germination, the protocorm is the first member to be forced out of the seed and it is followed first by the root and then by the stem. Thus the protocormal haustrum, because of its position, cannot be employed by the metacorm during germination as a functioning cotyledon. If any structure is to remain in contact with the tissue of the gametophyte, it devolves upon the appendages of the stem, and in Ginkgo we find the first two or three euphylls functioning as absorbing organs or pseudocotyledous.

Ginkgo undoubtedly shows, in its embryogeny, the most primitive condition of any of the gymnosperms, for it certainly shows the least specialization. In Cycas (Fig. 9) a less perfect protocorm is developed and in Zamia (Fig. 10) a further reduction of its bulk obtains. In fact it would seem that because of the positional relation of the blastema to the protocorm the latter cannot be made use of by the germinating embryo, and its disuse leads to an increasing limitation of the structure in gymnospermous embryogeny.

In the cycads, protocormal tissue directly behind the blastema, by rapid growth, carries the metacormal bud down into the tissue of the gametophyte (Figs. 9 and 10). This structure, the suspensor, becomes an organ of importance and is retained by all of the Coniferales. Their protocorms, however, consist of little more than a suspensor at the tip of which the metacormal primordia are differentiated (Fig. 11).

The suspensor of a gymnosperm embryo is clearly not homologous to that of a lycopod or angiosperm embryo. In the gymnosperms, the suspensor is developed between the body of the protocorm and the blastema and by its elongation serves to separate these two structures. In the lycopods and angiosperms, it is an outgrowth from the protocorm and has one free end. In these embryos the metacormal axis is differentiated through the body of the protocorm.

Polyembryony sometimes occurs in both gymnosperms and angiosperms through the production of two or more blastemata by one protocorm.

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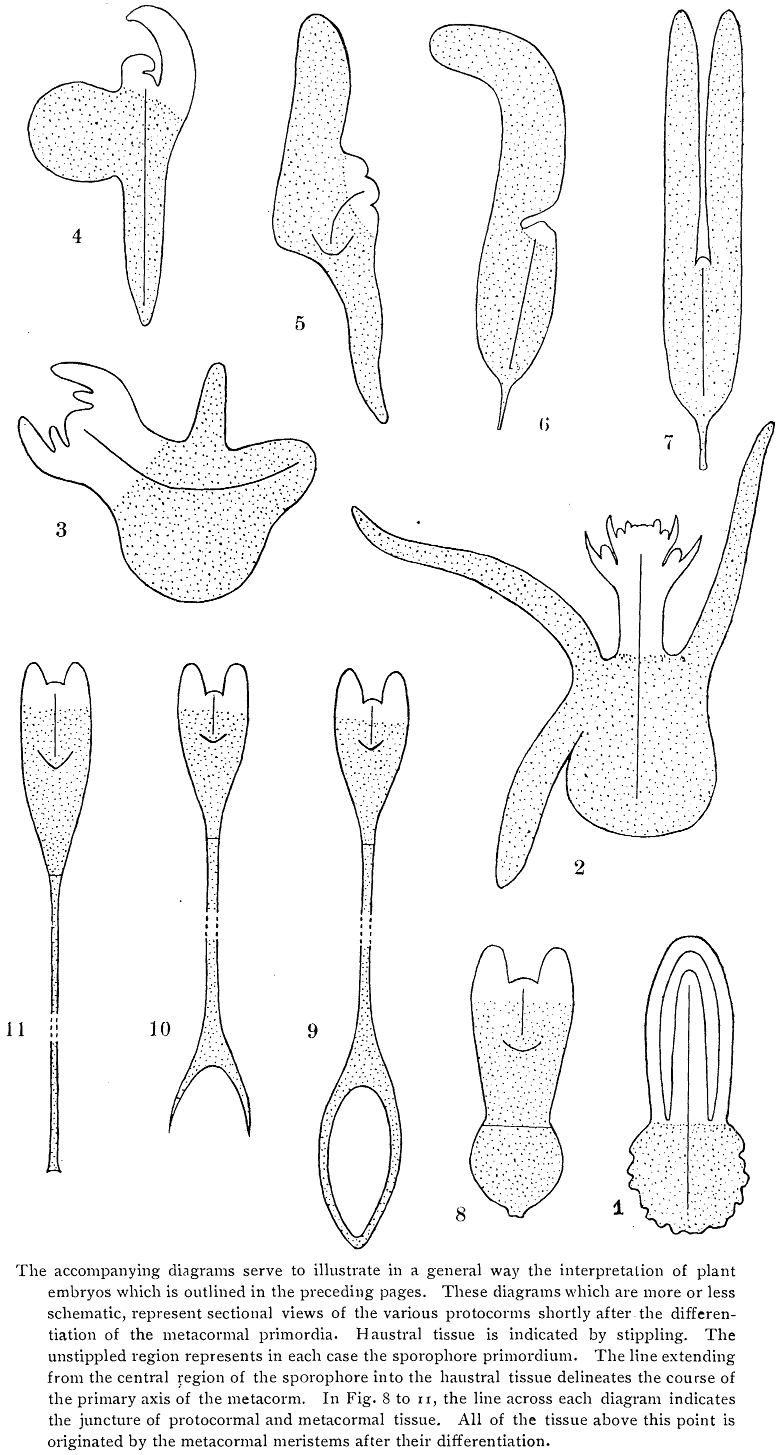

The accompanying diagrams serve to illustrate in a general way the interpretation of plant embryos which is outlined in the preceding pages. These diagrams which are more or less schematic, represent sectional views of the various protocorms shortly after the differentiation of the metacormal primordia. Haustral tissue is indicated by stippling. The unstippled region represents in each case the sporophore primordium. The line extending from the central region of the sporophore into the haustral tissue delineates the course of the primary axis of the metacorm. In Fig. 8 to 11, the line across each diagram indicates the juncture of protocormal and metacormal tissue. All of the tissue above this point is originated by the metacormal meristems after their differentiation.

1. Anthoceros. 2. Phylloglossum. 3. Selaginella. 4. Pteris. 5. Zeamais. 6. Alisma. 7. Bursa. 8. Ginkgo. 9. Cycas. 10. Zamia. 11. Pinus.